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DIGENETIC TREMATODES IN CEPHALOPODS

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(Text-figs. 1–2)

In addition to listing digenetic trematodes found in cephalopods, we provide descriptions of adults of *Derogenes varicus* and larvae of *Lecithochirium microstomum*, *Lecithochirium* sp., *Elytrophallus* sp., *Monilicaecum* sp., and *Stephanochasmus* sp. Only the first had been described previously from cephalopods, and the last represents the first record of a nonpiscine second intermediate host for a species of *Stephanochasmus*. We found 15 species infected, which brings to nearly 30 the total number of squids, octopods, and cuttlefish reported to be infected with Digenea. Many early records of trematodes in cephalopods are actually reports of Monogenea, Cestoda, or reproductive organs of cephalopods, and these are reviewed.

Our records suggest that cephalopods may serve as second intermediate or final hosts for trematodes such as *Stephanochasmus* sp. and *D. varicus*, respectively. More usually, cephalopods act as paratenic hosts capable of being important and, presumably, sometimes vital links in the completion of life cycles of some Digenea. In this way, they fulfill the role of piscine hosts with equivalent food preferences and parasites. Adults of all the worms discussed are parasites of fishes.

INTRODUCTION

Cephalopod molluscs have attracted little attention as potential hosts for digenetic trematodes. Though none appears to serve as a first intermediate host, many do act as second intermediate, paratenic, or final hosts. Hence, they probably play a more important role in the life history and dissemination of Digenea in the marine environment than is generally recognized.

In many respects, cephalopods resemble fish in their patterns of parasitic infections. This resemblance perhaps is evidenced most strikingly when comparing the trematode parasites of both groups. Not only do cephalopods, which have been recognized as carnivores at least since the time of Aristotle (Packard, 1972), feed on the same food as fishes, but in many cases they consequently acquire the same digeneans. Also, cephalopods function as paratenic hosts by feeding on infected fishes or their prey and retaining the worms without any further development of the parasites. Only a few digeneans of cephalopods, such as *Stephanochasmus* sp. reported below, infect their hosts by active invasion of cercariae.

The historical study of trematodes infecting cephalopods is complicated by lack of adequate descriptive information for both the hosts and the parasites. As a consequence, a great deal of taxonomic confusion exists. Many of the early reports included descriptions of organisms which upon subsequent examination proved to be larval cestodes, dicyemid mesozoans, or even parts of the cephalopod. In 1761, Linnaeus described

Fasciola barbata Linnaeus from *Loligo vulgaris* Lamark. Dollfus (1923*b*, 1942, 1958) later indicated that this parasite is probably a tetrarhynch cestode of the genus *Nybelinia* Poche. Dollfus (1923*b*) and others believed that *Distoma todari* Delle Chiaje was a larval cestode, whereas Kölliker (1849*b*) maintained that it was a dicyemid. The terms *Monostoma* and *Amphistoma*, usually applied to trematodes, have, when reporting worms from cephalopods, been incorrectly applied to larval cestodes or even cephalopod parts.

The detachable copulatory arm of certain octopods generated considerable debate in the literature. When Delle Chiaje (1825) discovered a small, wormlike body attached to a female argonaut, he concluded that it was a parasitic helminth and named it *Trichocephalus acetabularis*. Several years later, Cuvier (1829, 1830*a*, *b*) had the opportunity to examine additional material. He rejected Delle Chiaje's identification of it as a nematode and favoured, instead, aligning these parasites with the trematodes. Because of the multiplicity of suckers and the resemblance to a cephalopod arm, he erected the genus *Hectocotylus* Cuvier to contain species found on *Argonauta argo* (Linnaeus) and *Tremoctopus violaceus* Delle Chiaje. Cuvier's reputation was sufficient to assure most scientists at that time that the description was correct. Later, Dujardin (1845) questioned the exact nature of their affinities and arranged the species of *Hectocotyli* among the doubtful trematodes in his *Histoire Naturelle des Helminthes*. Kölliker (1845 to 1849) further complicated the story by proposing that these minute parasitic organisms actually represented males of the octopods in question. It was not until 1853 (*a*, *b*), that Müller demonstrated the true nature of these 'parasitic worms'. To this day, the modified copulatory arm of male cephalopods, whether detachable or not, is still referred to as the 'hectocotylus'.

In this paper, we describe one adult and five metaceracariae that all infect specific fishes as adults. Only one of those larvae had been reported previously from cephalopods. The paper also adds to and updates Dollfus' (1958) review of the digenetic trematodes of cephalopods, listing numerous new host-records and substantiating the importance of cephalopods as hosts for piscine digeneans (see Appendix 1). The appendix lists all known digeneans from cephalopods, including some new records which we were unable to examine, and two that were previously unidentified in a thesis by Mercer (1968). Monogenetic trematodes such as *Isancistrum loliginis* Beauchamp and *Polystoma loliginum* Delle Chiaje also have been reported and collected from cephalopods, but we will restrict this report to digenetic trematodes.

METHODS AND MATERIALS

Most of the cephalopods were examined fresh and their trematodes prepared under minimal coverslip pressure using several different methods. Cold AFA (alcohol–formalin–acetic acid) was used to fix worms from *Sepia officinalis*, *Abraliopsis falco*, *A. felis*, *Loliolopsis chiroctes*, *Pterygioteuthis gemmata*, *P. giardi*, *Japetella heathi*, and *Dosidicus gigas*; hot AFA, for those from *Lolliguncula brevis*; and 10% formalin, for those from *Octopus briareus* donated by Edward S. McSweeny. Robert B. Short loaned us stained specimens from *O. maorum*, and M. C. Mercer allowed us to use his data on trematodes from *Rossia* spp. We stained our material with Van Cleave's or Harris's hematoxylin and drew figures with the aid of a camera lucida. The worms occurred in the lumen of the organs unless cited as embedded. All measurements in descriptions are in microns unless otherwise indicated. Measurements of the hosts' dorsal mantle lengths precede DML throughout the text.

HEMIURIDAE

Derogenes varicus (Müller, 1784) Looss, 1901

Fig. 1 *A*, *B*

Data based on 19 mature specimens: Body fusiform, smooth, 672–1856 long by 325–620 wide at or near the acetabular, or widest, level. Preoral lobe present. Oral sucker 109–178 long by 116–194 wide. Acetabulum 202–323 long by 197–320 wide. Sucker-width ratio 1:1·4–1·8. Forebody 32–52% of body length. Prepharynx absent. Pharynx 46–71 long by 46–80 wide. Oesophagus as long as or longer than pharynx depending on state of contraction when fixed, though often indistinct. Caeca swollen, typically extending beyond vitellaria. Testes smooth, symmetrical or diagonal, separated from acetabulum, 78–174 long by 52–139 wide. Genital atrium short; pore either to left or right of midline of body between level of pharynx and slightly posterior to intestinal bifurcation. Sinus sac spherical to subspherical, with complete muscular wall, forming muscular cone distally; containing metraterm and male duct which unite at level of cone to form hermaphroditic duct, and numerous small cells surrounding ducts. Prostatic duct long, occasionally sinuous, surrounded by numerous elongated prostatic cells free in parenchyma. Seminal vesicle at or near anterior border of acetabulum usually smaller but sometimes larger than pharynx. Ovary smooth, post-testicular, sinistral or dextral, 64–203 long by 75–131 wide. Vitellaria two rounded compact masses, usually posterior to and either contiguous with or slightly separated from ovary; vitellarium usually larger than, but occasionally same size as, single testis. Seminal receptacle usually small and indistinct. Eggs thick-shelled, operculate, non-filamented, 41–58 long by 25–38 wide.

Host: *Sepia officinalis* Linnaeus, 1758.

Site: Rectum, near entrance of duct from ink-sac.

Intensity, incidence, and localities: 1–9 worms in 7 of 12 cuttlefish (105–146 mm DML) in Plymouth Sound and adjacent water, England.

Specimen deposited: University of Nebraska State Museum, Manter Laboratory No. 20063.

Discussion

Five additional specimens, 505–963 μm long, did not contain eggs. We found both mature and immature specimens coated with ink and consistently adjacent to the entrance of the duct from the ink sac. Because the taxonomy of *Derogenes varicus* and related species is confused, because the cuttlefish can act as a definitive host, and because variations in characters may be influenced by the cuttlefish, we have included detailed supplementary descriptive data.

Our specimens agree with most aspects of descriptions of *Derogenes varicus*, but some differ in several of the features presented by Dawes (1946) which primarily reflect the descriptions of Lebour (1908) and Johnstone (1907) who described specimens from fishes off England. In our specimens the body is widest near the level of the acetabulum rather than in the posterior region; the diameter of the acetabulum is consistently less than twice that of the oral sucker and usually located anterior rather than posterior to the midbody; the oesophagus is usually longer, not shorter, than the pharynx; the

genital pore occasionally is situated at the pharyngeal level rather than consistently posterior to the intestinal bifurcation; the sinus sac has a complete muscular wall as indicated by Odhner (1905), rather than a rudimentary incomplete one as described by Lloyd (1938) and referenced by Dawes; the testes are often symmetrical rather than

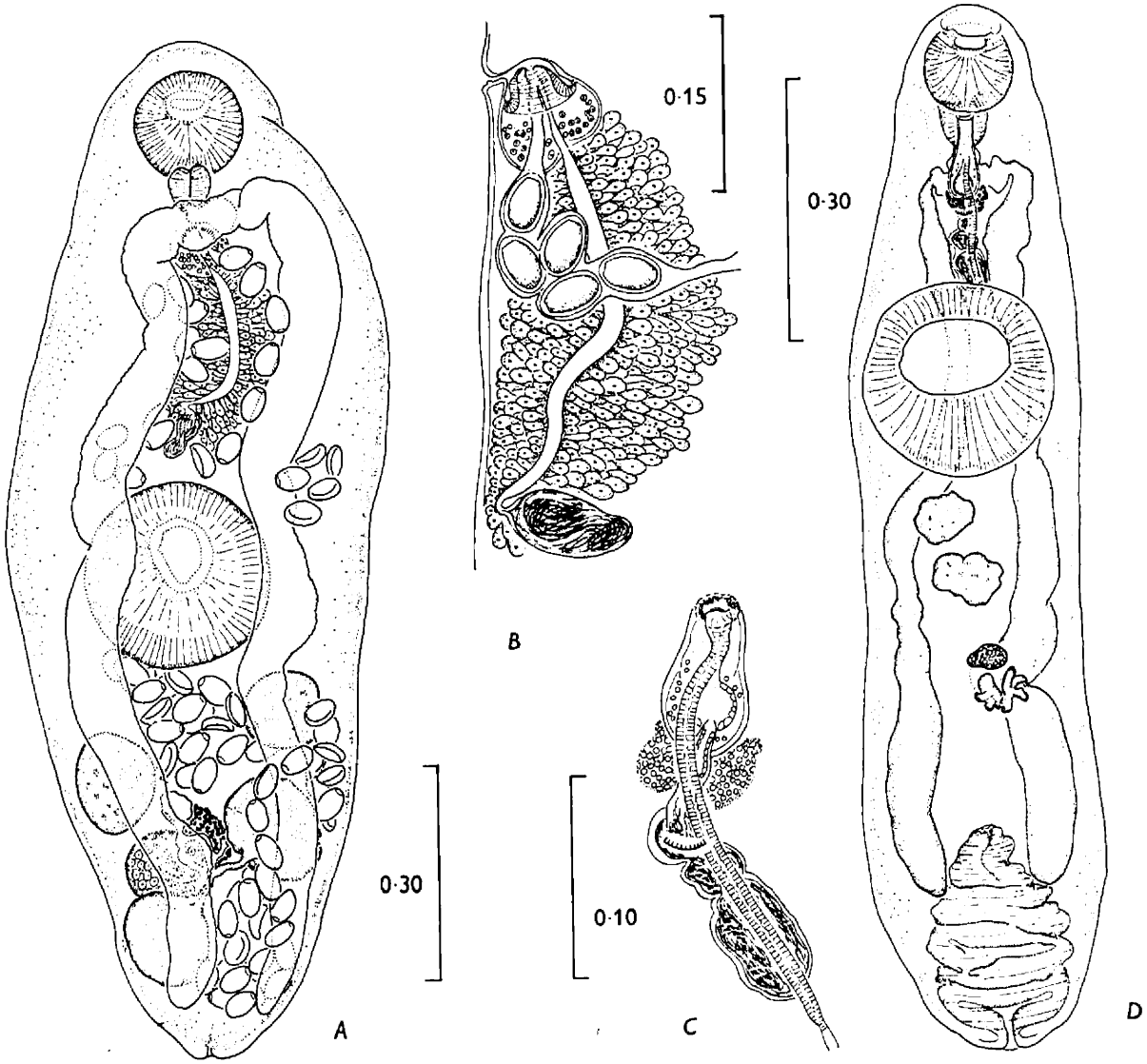

Fig. 1. *A–B, Derogenes varicus* from *Sepia officinalis*, *A*, whole specimen, dorsal view; *B*, terminal genitalia, lateral view; *C–D, Lecithochirium microstomum* from *Lolliguncula brevis*; *C*, terminal genitalia and preacetabular pit, ventral view; *D*, whole specimen, ventral view. Scale values are mm.

consistently diagonal; and the prostatic complex may extend to the anterior border of the acetabulum rather than just midway between the genital pore and acetabulum. In these respects, our specimens compare more favourably with the small ones described from Antarctic fishes by Prudhoe & Bray (1973). Brinkmann (1967), apparently not accepting the synonymy presented by Dawes, described *D. robustus* Brinkmann from one specimen. That specimen had unlobed vitellaria as those in our and Dawes's descriptions. It, however, differs from our worms by having a post-equatorially located acetabulum which has a diameter more than twice that of the oral sucker.

Two papers deal with unidentified worms in the cuttlefish similar to ours. Gros (1847) included a vague description and discussion, with some illustrations. Vaullegeard (1896) obtained his trematodes from the same site as ours in hosts also from the English Channel. He presented a brief description and an illustration which agreed with ours in most respects; however, apparently he omitted the testes from his illustration and labelled the vitellaria as such, and he presented a higher value for the diameter of the pharynx than illustrated. We believe that both the above authors had mature *Derogenes varicus*. Reimer (1974), in an abstract, also reported mature individuals from cuttlefish.

Invertebrate hosts in addition to cuttlefish also harbour trematodes identified as, or probably, *Derogenes varicus*. These hosts include copepods (Hall, 1929; Dollfus, 1955), a hermit crab (Uspenskaja, 1963), an annelid (Levinsen, 1881; Ditlevsen, 1917), and chaetognaths (Leuckart & Pagenstecher, 1858; Lebour, 1917; Hutton, 1954; Zaika & Kolesnikov, 1967; Kulachkova, 1970; Reimer *et al.*, 1971). In some of these hosts, such as the copepod *Lernaeocera lusci* (Bassett-Smith), the hermit crab *Pagurus pubescens* Krøyer, and the chaetognath *Sagitta bipunctata* Quoy & Gaimard, eggs were present in the trematodes as they are in our specimens. Specimens reported by Uspenskaja (1963) in a hermit crab from the Barents Sea were 3·4–3·9 mm long.

The Marine Biological Association (1957) listed a number of fishes which harbour this hemiurid in the vicinity of Plymouth, England, where the cuttlefish was collected. Doss (1964) cited most host-fishes from other localities. It occurs almost worldwide in shallow, cold-water fishes and in relatively deep-water fishes, causing Manter (1966) to consider it 'perhaps the most widely distributed of all animals. . . .'

Lecithochirium microstomum Chandler, 1935

Fig. 1*C*, *D*

Data based on 11 mounted specimens: Body 862–1445 long. Ecsoma short, retracted in fixed specimens. Preacetabular pit without conspicuous glands. Oral sucker 78–102 long by 87–113 wide. Acetabulum 188–267 long by 200–290 wide. Sucker-width ratio 1:2·0 to 2·7. Forebody 22–26% of body length. Sinus sac-length to acetabular-width ratio 1:2·9–4·1. Seminal vesicle typically tripartite. Testes slightly to considerably diagonal; anterior testis either dextral or sinistral. Vitelline lobes longer than wide. Excretory vesicle bifurcating immediately posterior to acetabulum with arms uniting dorsally near pharyngeal level.

Host: *Lolliguncula brevis* (Blainville, 1823).

Sites: Lumen of and embedded in wall of stomach and caecum.

Intensity, incidence, and localities: one worm in 11 and two in 1 of 138 squid (50–87 mm DML), none in 73 squid less than 50 mm long. All from Mississippi Sound and adjacent water.

Specimen deposited: University of Nebraska State Museum, Manter Laboratory No. 20064.

Discussion

One specimen of *Lecithochirum microstomum* had a few recently formed eggs 17 μm long by 9 μm wide. We doubt that many, if any, viable eggs are deposited by this trematode while present in the squid. Adult worms occur in the northern Gulf of Mexico in large numbers in the stomach of the prevalent cutlassfish, *Trichiurus lepturus* Linnaeus, as well as lesser numbers in numerous other fishes. The squid probably acquires its infection, serving as a paratenic host, from feeding on the bay anchovy, *Anchoa mitchilli* (Valenciennes), or other fishes. We have found immature *L. microstomum* in the alimentary tract of a low percentage of the bay anchovy in Mississippi Sound. Smaller and less-developed specimens of either that or a similar species of *Lecithochirium* Luhe also were observed more commonly in and near the air bladder of the dusky anchovy, *A. lyolepis* (Evermann & Marsh), in Biscayne Bay, Florida. Remains of fishes were found by us in many of the examined *Lolliguncula brevis*. Adrian R. Lawler, Richard W. Heard, and the senior author have observed on several occasions squid under lights at night feeding on anchovies and silversides at the Gulf Coast Research Laboratory.

Nasir & Díaz (1971) considered *Lecithochirum microstomum* a synonym of *L. rufoviride* (Rudolphi), a species for which Wagener (1860) reported immature specimens infecting cephalopods and other lower forms of marine life. We do not agree with their synonymy, and consider the discrepancy in sucker-ratios as just one difference between the two species.

Lecithochirium sp.

Data based on seven immature mounted specimens, one later sectioned. Body 1282–2291 long by 534–777 wide; ecsoma withdrawn into body in all specimens. Oral sucker 145–160 long by 174–197 wide, no conspicuous paired muscular lobes within oral cavity. Acetabulum 258–362 long by 278–373 wide. Sucker-width ratio 1:1·5–1·9, higher ratios in longer worms. Forebody 25–31% of body length. Preoral lip present. Preacetabular pit conspicuous, associated gland-cells not evident, usually midway between levels of acetabulum and pharynx. Pharynx 81–113 long by 87–110 wide. Testes slightly diagonal, near acetabulum, not well developed. Genital pore inconspicuous, located either medially or submedially at pharyngeal level. Sinus sac slightly longer than pharynx, incompletely developed. Prostatic cells located in area adjacent to hermaphroditic duct and in area posterior to junction of male and female ducts; seminal vesicle revealing indications of being tripartite in sectioned specimen; entire terminal genitalia incompletely developed.

Host: *Octopus maorum* Hutton, 1880.

Site: Embedded in wall of stomach.

Intensity and locality: seven in 1 octopus (about 15 cm DML) from Kaikoura Peninsula, New Zealand.

Specimen deposited: University of Nebraska State Museum, Manter Laboratory No. 20065.

Discussion

Because of the lack of well-developed terminal genitalia and no vitellaria or eggs, this worm can not be identified to a specific level. The generic identification is based primarily

on the presence in the specimens of a preacetabular pit and an incompletely developed sinus sac. Hewitt & Hine (1972) listed four species of *Lecithochirium* from New Zealand, but none agrees in all aspects with the one reported here.

?*Elytrophallus* sp.

Data based on one incompletely developed metacercaria. Body 951 long, smooth, with short, retracted ecsoma. Oral sucker folded during fixation, approximately 90 wide. Acetabulum 177 long by 180 wide. Forebody 22% of body length. Pharynx 81 long by 70 wide. Oesophagus short. Ceca extending to near posterior end of body. Testes diagonal; left testis 41 μm post-acetabular, 29 long by 61 wide; posterior testes dextral, genital pore submedian, dextral, at pharyngeal level; genital sinus extending posteriorly to short distance beyond pharyngeal level. Sinus sac extending from genital sinus diagonally almost to mid-acetabulum at left side; containing non-coiled, muscular sinus organ. Pars prostatica not fully developed, sinuous, joining uterus and muscular, saccular seminal vesicle near posterior border of acetabulum. Ovary short distance posterior to right testis. Vitellaria incompletely developed. Excretory arms apparently uniting anteriorly.

Host: *Japetella heathi* (Berry, 1911).

Site: Stomach.

Incidence and locality: one worm in 1 of 24 octopods (11–90 mm DML) from Gulf of California, La Pas Basin, Mexico, 24°20′ N; 110°05′ W, between 0–400 m.

Discussion

The structure of the terminal genitalia, though incompletely developed and difficult to interpret, forms the basis for this tentative identification. Additional specimens from *Japetella heathi* should provide necessary material to confirm or reject the identification.

DIDYMOZOIDAE

Monilicaecum sp.

Fig. 2*A*, *B*, *C*

Measurements based on 16 wholemounts and additional data based on observations of 214 living specimens: Body 89–337 long by 19–73 wide near acetabular, or widest level; 1·6–5·6 times longer than wide, filled with vesicular parenchyma. Tegument thick, smooth. Internal pseudosegmentation conspicuous. Oral sucker 23–40 long by 13–22 wide, often fixed partially protruded; composed of outer, thin layer of longitudinal and inner thick layer of circular muscles, portion of inner area with large vesicular cells. Acetabulum 22–41 long by 17–28 wide. Sucker-length ratio 1:0·6–1·2. Suckers overlapping to 69 apart, ratio of distance between suckers to body length (excluding small specimens with overlapping suckers) 1:4·0–7·4. Forebody 35–109 long; 23–42% of body length. Pharynx 5–10 long by 5–11 wide, inner part non-muscular and composed of vesicular cells, contiguous with oral sucker. Oesophagus with anterior portion thin walled, sinuous; posterior portion thick walled (6–13 thick), muscular, 20–40 long by 15–29 wide, forming 'stomach', anterior to or at level of acetabulum. Caeca descending

in undulating moniliform fashion; with 5–10 smooth, thin-walled, inflated chambers per caecum; those nearest stomach filled with fluid or glandular secretion; terminating 12–55 from posterior end of body. Testicular anlagen two, distinctive in all but smallest specimens, 7–11 long by 4–7 wide. Excretory pore terminal.

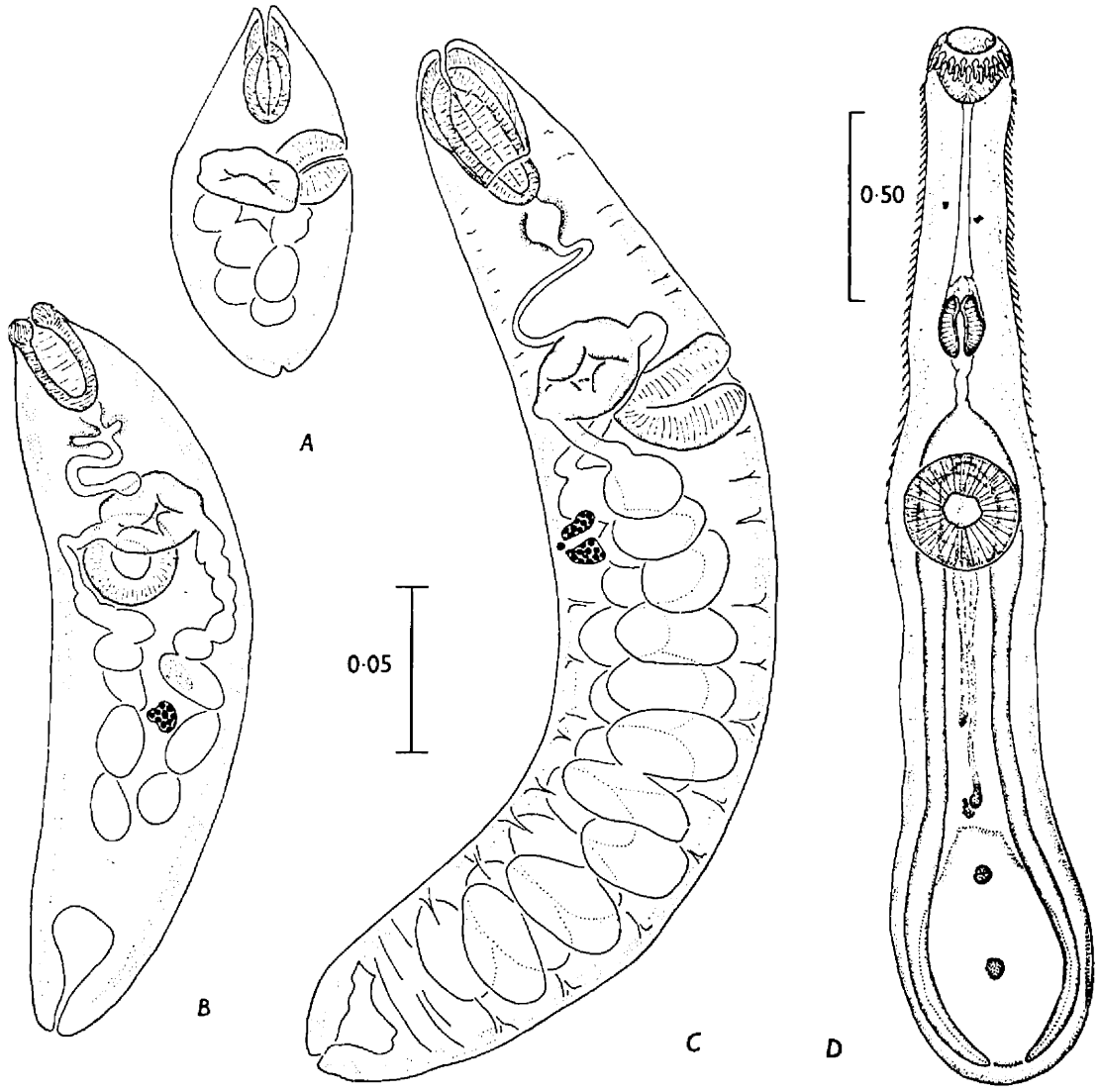

Fig. 2. *A–C*, *Monilicaecum* sp., *A*, recently hatched individual from *Abraliopsis falco*, dorsolateral view, note absence of testicular anlagen; *B*, medium-sized individual from *Pterygioteuthis giardi*, dorsal view; *C*, large individual from *Abraliopsis falco*, dorsolateral view; *D*, *Stephanochasmus* sp. from *Octopus briareus*, whole specimen, ventral view. Scale values are mm.

Hosts: *Loliolopsis chiroctes* Berry, 1929; *Abraliopsis falco* Young, 1972; *A. felis* McGowan & Okutani, 1968; *Pterygioteuthis gemmata* Chun, 1908; *P. giardi* Fischer, 1895; *Dosidicus gigas* (d'Orbigny, 1835).

Sites: Caecum and intestine.

Intensity, incidence, and localities: 1–5 worms in 38 of 234 *Pterygioteuthis giardi* (5–27 mm DML); 1–8 in 10 of 13 *Abraliopsis falco* (11–32 mm DML); 2 in 1 of 36 *Pterygioteuthis gemmata* (7–37 mm DML); 1–5 in 4 of 38 *Abraliopsis felis* (8–51 mm DML); 2–8 in 15 of 24 *Loliolopsis chiroctes* (30–82·5 mm DML); and 1–15 in 10 of 14

Dosidicus gigas (7·5–206 mm DML) in central and eastern North Pacific Ocean and Gulf of California.

Specimen deposited: University of Nebraska State Museum, Manter Laboratory No. 20066.

Discussion

Yamaguti (1942) erected *Monilicaecum ventricosum* for a larval trematode of uncertain affinities. The name *Monilicaecum* Yamaguti remains in use, but as a collective larval-group-name. It usually refers to larval didymozoids possessing a 'stomach' at the caecal bifurcation and having chambered caeca. Since Yamaguti's original description, several forms have been described from hosts other than cephalopods. Nikolaeva (1965, 1970) described two forms; Reimer *et al.* (1971) briefly described one; and Fischthal & Kuntz (1964) and Fischthal & Thomas (1968) described a total of six more that they associated with the group-name *Monilicaecum*, even though only one, 'Didymozoid F', in the latter paper had the prominent stomach found in the others described, including ours. Several additional papers refer specifically to didymozoids in cephalopods. Dollfus (personal communication) told us that what he had reported from *Illex coindetii* (see Appendix 1) was probably a form of *Monilicaecum*; Reimer (1974) reported an undescribed didymozoid larva from *Ommastrephes sagittatus*; and Fields & Gauley (1972) mentioned an undescribed didymozoid metacercaria from *Symplectoteuthis oualaniensis* captured in the eastern tropical Pacific Ocean.

Our form is smaller than most other forms of *Monilicaecum* and the only one known to possess genital anlagen. It also differs from them by having the width of its acetabulum approximately the same size or larger than the width of the stomach, rather than considerably less. That relationship was not given for the larva described by Reimer *et al.* (1971), but from their illustration, it appears similar to ours. That worm, even though short like ours (226–326 μm), can be differentiated from it by having an inconspicuous stomach surrounded by numerous large cells. The only other reference to a *Monilicaecum* larva approximating ours in size was that of Nikolaeva (1965). Her recorded specimens were 360–567 μm long and additionally differed from ours in having a relatively shorter forebody. Some larger specimens described by Fischthal & Thomas (1968) were tentatively called the same form, but those authors suggested that it possibly represented a different species.

Thanks to Dr Leo Margolis of the Pacific Biological Station, Nanaimo, British Columbia, we had the opportunity to examine seven specimens of the larva mentioned by Fields & Gauley (1972). The *Monilicaecum* sp. measured 459–569 μm and had a forebody 34–39 % of the body length. Considering the size and shape of the suckers and the number of chambered caeca, the specimens were similar to ours. Even though difficult to examine, the stomach was nearly as wide as the worm and not muscular like in our specimens. Also, testicular anlagen could not be seen, and we consider the specimens different than those we described.

Rather than the squids acquiring their infections from fishes as they apparently do for some of the other trematodes, the didymozoid could have been transmitted from copepods. Madhavi (1968) cited a metacercaria in a copepod from the Bay of Bengal

that was considered under the collective larval-group-name *Premonilicaecum* by Yamaguti (1971). From the North Sea, Reimer *et al.* (1971) reported the copepod *Calanus finmarchicus* (Gunnerus) as an intermediate host containing a non-encysted larva as well as a chaetognath, polychaete, ctenophore, and six coelenterates as paratenic hosts. We observed excysting larvae, the same size as we show for the smallest illustrated (Fig. 2*A*), in squid stomachs along with well-crushed crustacean parts. Also, *Paracalanus aculeatus* Giesbrecht, the copepod host cited by Madhavi (1968), occurs in the same localities as our infected squid. Whether the squids acquired their infections from a copepod, fish, mollusc, or other hosts, they, by being a common item of prey, probably play an important role in transmitting the parasite to the carnivorous definitive piscine host.

Monilicaecum larvae, as suggested earlier, comprise several different species, and our belief that the form described here represents only a single species is conjecture. According to Yamaguti (1970), even different didymozoid larval groups can develop into adults belonging to the same genus. A *Postmonilicaecum* larva seemed to develop into *Didymocystis superpalati* Yamaguti, whereas *D. irregularis* Yamaguti developed from a *Posttorticaecum* form.

STEPHANOCHASMIDAE

Stephanochasmus sp.

Fig. 2*D*

Description based on 5 mounted metacercaria: Metacercarial cyst thin, transparent; surrounded by thickened opaque host-tissue rendering infection easily visible with naked eye. Body 1102–3316 long. Tegumental spines conspicuous and dense in forebody, usually small and sparse in hindbody. Peribuccal spines 32–84 long, in two alternate uninterrupted rows totaling 36–44 in number; dorsal, ventral, oral, and aboral spines approximately equal in some specimens but dorsal aboral spines tending to be slightly longer on majority. Oral sucker 131–261 wide. Acetabulum 159–350 wide. Sucker-width ratio 1:1·2–1·6. Pharynx 110–201 long by 73–144 wide. Prepharynx about 3 times and oesophagus more than $\frac{1}{2}$ times length of pharynx. Eyespots concentrated in four specimens and dispersed in one along level of prepharynx. Excretory vesicle ovoid, extending anterior to testicular anlagen. Uroproct not observed.

Host: *Octopus briareus* Robson, 1929.

Sites: Encysted primarily in mantle cavity, but also in intestinal mesentery and in tissue adjacent to arteries of gills.

Intensity, incidence, and locality: five and eight specimens in 2 of 2 hosts (50–70 mm DML) from Key Largo, Florida, and two in 1 of 3 from Biscayne Bay, Florida.

Specimen deposited: University of Nebraska State Museum, Manter Laboratory No. 20067.

Discussion

Our specimens appear in most respects like *Stephanochasmus tenue* (Linton), except the peribuccal spines range between 36 and 44 in number rather than being reasonably

constant at 42, and the relative size of the pharynx is not as large as indicated by Martin (1939) in his life-history study of the species. The life cycle of *S. tenue* worked out by Martin (1939) included the Atlantic silverside, *Menidia menidia* (Linnaeus), which probably does not constitute a dietary item for the octopus. Our specimens, however, compare especially well with the illustration of a worm identified by Stunkard (1961) as *S. tenue* excysted from *Fundulus heteroclitus* (Linnaeus). Since considerable confusion exists concerning the taxonomy of many members of the genus, we refrain from identifying our metacercaria. This report constitutes the first time any member of the genus *Stephanochasmus* (= *Stephanostomum*) has been reported from a nonpiscine host. Yamaguti (1971) misquoted Nicoll & Small (1909) as reporting *S. baccatum* (Nicoll) from a crab rather than the dab, *Pleuronectes limanda* Linnaeus.

Following Dollfus (1973), we place *Stephanochasmus* Looss in the family Stephanochasmidae Nicoll, which is characterized by the presence of an I-shaped excretory vesicle rather than a Y-shaped one, as in the acanthocolpids.

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APPENDIX 1. CEPHALOPODS HARBOURING DIGENETIC TREMATODES

Cephalopod	Digenean	Locality	References
O. SEPIOIDEA			
Rossia molleri Steenstrup	Mature hemiurid[1] HEMIURIDAE	Franklin Territory, Canada (Victoria Island)	M. C. Mercer, pers. comm.
Rossia sublaevis Verrill	Immature hemiurid[1] HEMIURIDAE	Newfoundland, Canada (Hermitage Bay)	M. C. Mercer, pers. comm.
Sepia officinalis Linnaeus	*Derogenes varicus* HEMIURIDAE	England (Plymouth)	Reimer (1974); Present paper
	Distome	France (Luc-sur-Mer)	Vaullegeard (1896); Dollfus (1958)
	Gonocercella sepiocola[2] HEMIURIDAE	English Channel, West Africa (?)	Reimer (1974)
Sepia sp.?	Distome (*D. varicus*)	Not indicated	Gros (1847); Dollfus (1958)
Sepiola aurantiaca Jatta	Unidentified digenean (specimen lost)	England (Plymouth)	Hochberg (unpublished data)
O. TEUTHOIDEA S. O. MYOPSIDA			
Alloteuthis subulata (Lamarck)	Unidentified digenean (specimen lost)	England (Plymouth)	Hochberg (unpublished data)
Loliolopsis chiroctes Berry	*Monilicaecum* sp. DIDYMOZOIDAE	Mexico (Gulf of California)	Hochberg (1969); Present paper
Lolliguncula brevis (Blainville)	*Lecithochirium microstomum* HEMIURIDAE	USA (Mississippi)	Present paper
S. O. OEGOPSIDA			
Abraliopsis falco Young	*Monilicaecum* sp. DIDYMOZOIDAE	Eastern and Central North Pacific Ocean; Gulf of California	Hochberg (1969); Present paper
Abraliopsis felis McGowan & Okutani	*Monilicaecum* sp. DIDYMOZOIDAE	Eastern North Pacific Ocean	Hochberg (1969); Present paper
Chiroteuthis veranyi (Ferussac) (as *Doratopsis vermicularis*)	*Lepocreadium album* LEPOCREADIIDAE (= *Cercaria setifera*)	Italy (Naples)	Dollfus (1958); Rebecq (1965) Monticelli (1914)
Dosidicus gigas (d'Orbigny) (as *Symplectoteuthis* of Hochberg)	*Monilicaecum* sp. DIDYMOZOIDAE	Mexico (Gulf of California)	Hochberg (1969); Present paper
Illex coindetii (Vérany)	*Monilicaecum* sp. DIDYMOZOIDAE	Monaco; France (Concarneau)	Dollfus (1971, and pers. comm.)
	(= *Pleorchis* sp.)		Dollfus (1958); Wirz (1958)

APPENDIX 1. (*cont.*)

Cephalopod	Digenean	Locality	References
Illex illecebrosus (Lesueur) (as *Ommastrephes illecebrosa*)	*Distomum* sp. (immature)	Canada	Stafford (1907)
Ommastrephes sp. ?	Unidentified digenean (adult)	Not indicated	Pelseneer (1928); Clarke (1966)
Pterygioteuthis gemmata Chun	*Monilicaecum* sp. DIDYMOZOIDAE	Eastern North Pacific Ocean	Hochberg (1969); Present paper
Pterygioteuthis giardi Fischer	*Monilicaecum* sp. DIDYMOZOIDAE	Mexico (Gulf of California)	Hochberg (1969); Present paper
Pterygioteuthis sp. ?	Unidentified hemiurid (specimen lost)	Eastern North Pacific Ocean	Hochberg (unpublished data)
Symplectoteuthis oualaniensis (Lesson)	*Monilicaecum* sp.[3] DIDYMOZOIDAE	Eastern Tropical Pacific Ocean	Fields & Gauley (1972)
Todarodes sagittatus (Lamarck) (as *Loligo todarus*, *Ommastrephes sagittatus*, and *O. todarus*)	*Distoma todari*[4,5]	Italy (Naples)	Delle Chiaje (1822, 1841); Blanchard (1847); Kölliker (1849*b*); Dollfus (1958)
	Didymozoidae metacercaria DIDYMOZOIDAE	West Africa (Rio de Oro)	Reimer (1974)
Todaropsis eblanae (Ball)	Unidentified didymozoid (specimen lost)	France (Banyuls-sur-Mer) Mediterranean Sea	Hochberg (unpublished data)
O. OCTOPODA S. O. INCIRRATA			
Argonauta argo Linnaeus	*Accacoelium pelagiae* ACCACOELIDAE (= *Distoma pelagiae*)	Italy (Messina)	Yamaguti (1971) Kölliker (1849*a*); Moulinié (1856); Monticelli (1893); Looss (1902); Dollfus (1960*a*, *b*, 1963); Nikolaeva (1968)
	(= *Distoma kollikerii*)[6]		Cobbold (1860)
	Referred to *Agamodistomum*		Parona (1912)
	Referred to *Orophocotyle*		Dollfus (1958); Wirz (1958)
	Referred to *Mneiodhneria*		Timon-David (1967, Thèse, Faculté Mixte de Médecine et de Pharmacie de Marseille)
Argonauta sp. ?	*Distomum dactylipherum* HEMIUROIDEA	Indian Ocean	Poirier (1885); Braun (1889–93); Buttel-Reepen (1902)
Eledone cirrhosa (Lamarck) (as *E. aldrovandi*)	Unidentified distome (immature)	Monaco	Dollfus (1958)
Japetella heathi (Berry)	? *Elytrophallus* sp. HEMIURIDAE	Gulf of California	Present paper
Octopus briareus Robson	*Stephanochasmus* sp. STEPHANOCHASMIDAE	USA (Florida Keys)	Present paper

APPENDIX 1. (*cont.*)

Cephalopod	Digenean	Locality	References
Octopus maorum Hutton	*Lecithochirium* sp. HEMIURIDAE	New Zealand (Kaikoura)	Present paper
	Plagioporus maorum OPECOELIDAE	New Zealand (Kaikoura)	Allison (1966); Short & Powell (1968); Yamaguti (1971)
Octopus vulgaris Lamarck (as *O. octopodia*)	*Distoma octopodis*	Italy (Naples)	Delle Chiaje (1822, 1829, 1841); Blanchard (1847); Carus (1885); Dollfus (1958)
	Ptychogonimus[7] *megastoma* PTYCHOGONIMIDAE	Italy (Naples)	Palombi (1942)
Robsonella australis (Hoyle)	*Plagioporus maorum* OPECOELIDAE	New Zealand (Portobello)	Short & Powell (1968)
'Cephalopod'	*Distoma krohnii*[8]	Not indicated	Kölliker (1849*b*)
'Cephalopods'	*Lecithochirium rufoviride* HEMIURIDAE (= *Distoma rufoviride*)	Not indicated	Dollfus (1958) Wagener (1860); Dollfus (1923*a*)

[1] Identified by Dr Sewell H. Hopkins of Texas A & M University.

[2] *Gonocercella sepiocola* Reimer, 1974, is a *nomen nudum* because it fails to satisfy conditions of Article 13a of the International Code of Zoological Nomenclature adopted by the XV International Congress of Zoology.

[3] Identified by Dr Leo Margolis of The Fisheries Research Board of Canada, Nanaimo, British Columbia.

[4] There is considerable confusion concerning this species. The general consensus is that it represents a larval cestode. See Monticelli (1892); Parona (1894); Dollfus (1923*b*); and Joyeux & Baer (1936). Kölliker (1849*b*) considered *D. todari* to be a dicyemid mesozoan.

[5] Misspelled '*D. totari*' by Blanchard (1847).

[6] Misspelled '*D. kolikerii*' by Cobbold (1860).

[7] Experimental infection; natural infections unknown; ingested metacercaria eliminated within 3 days.

[8] Misspelled '*Dystoma Krohnii*' by Kölliker (1849*b*).

REFERENCES

ALLISON, F. R., 1966. A new species of adult Allocreadidae from *Octopus maorum* Hutton. *Record of the Canterbury Museum*, **8**, 81–5.

BLANCHARD, E., 1847. Recherches sur l'organization des vers. *Annales des sciences naturelles, Zoologie*, Ser. 3, **8**, 271–341.

BRAUN, M. G. C. C., 1889–1893. Vermes. Ia. Mionelminthes, Trichoplax und Trematodes. In: *Klassen und Ordnungen des Thier-Reichs wissenschaftlich dargestellt in Wort und Bild*, ed. H. G. Bronn, vol. **4**, 209–925. Leipzig.

BRINKMANN, A., JR., 1967. Some trematodes from marine fishes in the waters of Rhodes. *Årbok for Universitetet i Bergen Matematisk-naturvitenskapelig serie*, for 1966, **10**, 1–13.

BUTTEL-REEPEN, H. B. VON, 1902. Zur kenntnis der Gruppe des *Distomum clavatum*, insbesondere des *D. ampullaceum* und des *D. siemersi*. *Zoologischer Jahresbericht. Zoologische Station zu Neapel*, **17**, 165–202.

CARUS, J. V., 1885. Vermes. In: *Prodromus faunae Mediterraneae* [*etc.*] vol. **1**, 112–282. Stuttgart.

CLARKE, M. R., 1966. A review of the systematics and ecology of oceanic squids. *Advances in Marine Biology*, **4**, 91–300.

COBBOLD, T. S., 1860. Synopsis of the Distomidae. *Proceedings of the Linnean Society of London, Zoology*, Ser. 17, **5**, 1–56.

CUVIER, G., 1829. Mémoire sur un ver parasite d'un nouveau genre (*Hectocotylus octopodis*). *Annales des sciences naturelles*, **18**, 147–56.

CUVIER, G., 1830*a*. Ueber einen Schmarotzerwurm einer neuen Gattung (*Hectocotylus octopodis*). *Notizen und Tagsberichte aus dem Gebiete der Natur- und Heilkunde*, **27**, 6–10.

CUVIER, G., 1830*b*. On parasitic animals, and on a new genus of that family. *Edinburgh New Philosophical Journal*, **22**, 101–4.

DAWES, B., 1946. *The Trematoda: with special reference to British and other European forms*. 644 pp. Cambridge: Cambridge University Press.

DELLE CHIAJE, S., 1822 [i.e., 1830 ?]. *Memorie sulla storia e notomia degli animali senza vertebre del regno di Napoli*, 34–109. [i.e., 114 pls.] Napoli: Fratelli Fernandes.

DELLE CHIAJE, S., 1825 [i.e., 1828 ?] Nota sul mollusco dell' *Argonauta argo*, su una nuova specie di epizoo che vi ospita, e sulla *Medusa velella*. In: *Memorie sulla storia e notomia degli animali senza vertebre del regno di Napoli*, vol. **2**, 219–45. Napoli: Fratelli Fernandes.

DELLE CHIAJE, S., 1829 [i.e., 1831 ?]. Su' cefalopedi [sic.] In: *Memorie sulla storia e notomia degli animali senza vertebre del regno di Napoli*, vol. **4**, 38–116, 151–2. Napoli: Fratelli Fernandes.

DELLE CHIAJE, S., 1841. *Descrizione e notomia degli animali invertebrati della Sicilia citeriore osservati vivi regli anni 1822–30*, vol. **3**, 1–142. Napoli: Stabilimento Tipografico di C. Batelli.

DITLEVSEN, H., 1917. Trematoder. *Meddelelser om Grønland*, **23**, 1143–52.

DOLLFUS, R. P., 1923*a*. Remarques sur le cycle évolutif des Hémiurides. *Annales de parasitologie humaine et comparée*, **1**, 345–51.

DOLLFUS, R. P., 1923*b*. Énumération des cestodes du plancton et des invertebrés marins. *Annales de parasitologie humaine et comparée*, **1**, 363–94.

DOLLFUS, R. P., 1942. Études critiques sur les Tétrarhynques du Muséum de Paris. *Archives du Muséum d'histoire naturelle Paris*, Ser. 6, **19**, 1–466.

DOLLFUS, R. P., 1955. Métacercaire progénétique de *Derogenes* (Trematoda, Hemiuroidea) chez un copépode parasite de poisson. *Vie et milieu*, **5** (for 1954), 565–8.

DOLLFUS, R. P., 1958. Copépodes, isopodes et helminthes parasites de céphalopodes de la Méditerranée et de l'Atlantique Européen. *Faune marine des Pyrénées-orientales*, **1**, 61–72.

DOLLFUS, R. P., 1960*a*. Distomes des chaetognathes. *Bulletin de l'Institut des pêches maritimes du Maroc*, **4**, 1–27.

DOLLFUS, R. P., 1960*b*. Critique des récentes innovations apportées à la classification des Accacoeliidae (Trematoda, Digenea). Observations sur des métacercaires de cette famille. *Annales de parasitologie humaine et comparée*, **35**, 648–71.

DOLLFUS, R. P., 1963. Liste des coelentérés marins, palaearctiques et indiens ou ont eté trouves des trématodes digénetiques. *Bulletin de l'Institut des pêches maritimes du Maroc*, **9–10**, 33–57.

DOLLFUS, R. P., 1971. Larves de Didymozooidae chez un cephalopode. In: *Proceedings of the second international congress of parasitology*, Sept. 6–12, 1970, Washington, D.C., **4**, 47–8. [Abstract]

DOLLFUS, R. P., 1973. Parasitologia mauritanica. Digénétiques de Téléostéens, 1re note. Du genre *Stephanochasmus* A. Looss, 1900 (Trematoda, Digenea). *Bulletin de l'Institut Fondamental d'Afrique Noire*, **34**, Sér. 4, 809–27.

DOSS, M. A., 1964. *Index-catalogue of medical and veterinary zoology*. Subjects: Trematoda and trematode diseases. Part 3: Supergenera and Genera D, pp. 359–595. Washington, D.C.: U S. Department of Agriculture, U.S. Govt. Printing Office, Washington, D.C.

DUJARDIN, F., 1845. *Histoire Naturelle des Helminthes ou Vers Intestinaux*. 645 pp. Paris.

FIELDS, W. C. & GAULEY, V. A., 1972. A report on cephalopods collected by Stanford Oceanographic Expedition 20 to the eastern tropical Pacific Ocean September to November, 1968. *Veliger*, **15**, 113–18.

FISCHTHAL, J. H. & KUNTZ, R. E., 1964. Digenetic trematodes of fishes from Palawan Island, Philippines. IV. Some immature didymozoidae, a bucephalid; a new hemiuroid genus and subfamily. *Journal of Parasitology*, **50**, 253–60.

FISCHTHAL, J. H. & THOMAS, J. D., 1968. Digenetic trematodes of marine fishes from Ghana; families Acanthocolpidae, Bucephalidae, Didymozoidae. *Proceedings of the Helminthological Society of Washington*, **35**, 237–47.

GROS, G., 1847. De la génération spontanée ou primitive en général et en particulier des helminthes. *Bulletin de la Société Impériale des Naturalistes de Moscou*, **20**, 517–40.

HALL, M. C., 1929. Arthropods as intermediate hosts of helminths. *Smithsonian Miscellaneous Collections*, **81**, 1–77.

HEWITT, G. C. & HINE, P. M., 1972. Checklist of parasites of New Zealand fishes and of their hosts. *New Zealand Journal of Marine and Freshwater Research*, **6**, 69–114 (Fisheries Research Publication No. 181).

HOCHBERG, F. G., 1969. Cephalopods as intermediate hosts for larval didymozoids. In: *American Society of Parasitologists*. Annual Meeting, Nov. 3–7, 1969, Washington, D.C., Program and Abstracts, p. 55. [Abstract]

HUTTON, R. F., 1954. *Metacercaria owreae* n. sp., an unusual trematode larva from Florida current chaetognaths. *Bulletin of Marine Science of the Gulf and Caribbean*, **4**, 104–9.

JOHNSTONE, J., 1907. Internal parasites and diseased conditions of fishes. *Proceedings and Transactions of the Liverpool Biological Society*, **21**, 270–303.

JOYEUX, C. & BAER, J. G., 1936. Cestodes. *Faune de France*, **30**, 1–613.

KÖLLIKER, A. VON, 1845. Some observations upon the structure of two new species of *Hectocotyle* parasitic upon *Tremoctopus violaceus*, Delle Chiaje, and *Argonauta Argo*, L.; with an exposition of the hypothesis that these *Hectocotyle* are the males of the Cephalopoda upon which they are found. *Proceedings of the Linnean Society of London*, **1**, 236–8.

KÖLLIKER, A. VON, 1846. Some observations upon the structure of two new species of *Hectocotyle*, parasitic upon *Tremoctopus violaceus*, D. Ch., and *Argonauta Argo*, Linn.; with an exposition of the hypothesis that these *Hectocotylae* are the males of the Cephalopoda upon which they are found. *Transactions of the Linnean Society of London*, **20**, 9–21.

KÖLLIKER, A. VON, 1849*a*. Zwei neue Distomen, *Distoma pelagiae* nov. sp. und *D. okenii* nov. sp. *Berichte von der Königlichen Zootomischen Anstalt zu Würzburg*, **2**, 53–8.

KÖLLIKER, A. VON, 1849*b*. Ueber *Dicyema paradoxum*, den Schmarotzer der Venenanhange der Cephalopoden. *Berichte von der Königlichen Zootomischen Anstalt zu Würzburg*, **2**, 59–66.

KÖLLIKER, A. VON, 1849*c*. *Hectocotylus argonautae* D. Ch. und *Hectocotylus tremoctopodis* Köll., die Männchen von *Argonauta argo* und *Tremoctopus violaceus* D. Ch. *Berichte von der Königlichen Zootomischen Anstalt zu Würzburg*, **2**, 67–89.

KULACHKOVA, V. G., 1970. [Helminths of *Sagitta elegans* in the White Sea.] In: *Voprosy morskoi parazitologii [All-Union symposium (1st) on parasites and diseases of marine animals, Sevastopol*, 1970]. Kiev: Izdat.

LEBOUR, M. V., 1908. Fish trematodes of the Northumberland coast. *Fisheries Officer's Reports, Northumberland Sea Fisheries Committee*, **1907**, 11–67.

LEBOUR, M. V., 1917. Some parasites of *Sagitta bipunctata*. *Journal of the Marine Biological Association of the United Kingdom*, **11**, 201–6.

LEUCKART, R. & PAGENSTECHER, A., 1858. Untersuchungen über niedere Seethiere. *Archiv für Anatomie, Physiologie und Wissenschaftliche Medicin*, **1858**, 558–613.

LEVINSEN, G. M. R., 1881. Bidrag til Kundskab om Grønlands Trematodfauna. *Oversigt over det K. Danske Videnskabernes Selskabs Forhandlinger*, **1**, 52–84.

LINNAEUS, C., 1761. *Fauna Suecica sistens animalia Sueciae regni: mammalia, aves, amphibia, pisces, insecta, vermes. Distributa per classes et ordines, genera et species* [etc.]. Editio altera, auctior. 578 pp. Stockholmiae.

LLOYD, L. C., 1938. Some digenetic trematodes from Puget Sound fish. *Journal of Parasitology*, **24**, 103–33.

LOOSS, A., 1902. Ueber die Gattung *Orophocotyle* n. g. (Zur Kenntnis der Trematodenfauna des Triester Hafens. 1). *Zentralblatt für Bakteriologie, Parasitenkunde Infektionskrankheiten und Hygiene (Jena)*, **31**, 637–44.

MADHAVI, R., 1968. A didymozoid metacercaria from the copepod, *Paracalanus aculeatus* Giesbrecht, from Bay of Bengal. *Journal of Parasitology*, **54**, 629.

MANTER, H. W., 1966. Parasites of fishes as biological indicators of recent and ancient conditions. In: *Host-parasite relationships*. Proceedings of the twenty-sixth annual biology colloquium, April 23–24, 1965, ed. J. E. McCauley, 59–71. Corvallis: Oregon State University Press.

MARINE BIOLOGICAL ASSOCIATION, 1957. *Plymouth Marine Fauna*, 3rd ed, 457 pp.

MARTIN, W. E., 1939. Studies on the trematodes of Woods Hole. II. The life cycle of *Stephanostomum tenue* (Linton). *Biological Bulletin. Marine Biological Laboratory, Woods Hole, Mass.*, 77, 65–73.

MONTICELLI, F. S., 1892. Studi sui trematodi endoparassiti, *Monostomum cymbium* Diesing. Contribuzione allo studio dei monostomidi. *Memorie della R. Accademia delle scienze di Torino*, Serie 2, **42**, 683–727.

MONTICELLI, F. S., 1893. Studii sui trematodi endoparassiti: Primo contributo di osservazioni sui distomidi. *Zoologische Jahrbücher. Supplement (Jena)*, **3**, 1–229.

MONTICELLI, F. S., 1914. Ricerche sulla *Cercaria setifera* di Joh. Müller. *Atti della R.Accademia delle scienze Fisiche e Matematiche (Napoli)*, Serie 2, **15**, 1–48.

MOULINIÉ, J. J., 1856. De la reproduction chez les trematodes endoparasites. *Mémoires de l'Institut Genevois*, **3**, 7–278.

MÜLLER, H., 1853*a*. Ueber das Männchen von *Argonauta Argo* und die Hectocotylen. *Zeitschrift für wissenschaftliche Zoologie*, **4**, 1–35.

MÜLLER, H., 1853*b*. Upon the male of *Argonauta Argo* and the *Hectocotyli*. In: *Scientific Memoirs, Selected from the Transactions of Foreign Academies of Science, and from Foreign Journals*, pp. 52–91. London: Taylor and Francis.

NASIR, P. & DÍAZ, M. T., 1971. A revision of genus *Lecithochirium* Luehe, 1901, and redescription of *L. monticellii* (Linton, 1898) Skrjabin and Guschanskaja, 1955. *Rivista di Parassitologia*, **32**, 27–36.

NICOLL, W. & SMALL, W., 1909. Notes on larval trematodes. *Annals and Magazine of Natural History*, Series 8, **3**, 237–46.

NIKOLAEVA, V. M., 1965. [On the development cycle of trematodes belonging to the family Didymozoidae (Monticelli, 1888) Poche, 1907. *Zoologicheskiĭ zhurnal*, **44**, 1317–27. [In Russian]

NIKOLAEVA, V. M., 1968. [On finding Accacoeliidae larvae in the fishes and invertebrates.] *Akademiya Nauk Ukrainskoi* SSR. *Institut Biologii Yuzhnÿka Morei im. A. O. Kovalevskogo, Biologiya Morya, Kiev*, **14**, 83–9.

NIKOLAEVA, V. M., 1970. [Didymozoidae metacercaria in Red Sea fishes.] *Akademiya Nauk Ukrainskoi SSR. Institut Biologii Yuzhnÿka Morei im. A. O. Kovalevskogo, Biologiya Morya, Kiev*, **20**, 113–29. [In Russian]

ODHNER, T., 1905. Die Trematoden des arktischen Gebietes. *Fauna arctica*, **4**, 291–372.

PACKARD, A., 1972. Cephalopods and fish: the limits of convergence. *Biological Reviews*, **47**, 241–307.

PALOMBI, A., 1942. Il ciclo biologico di *Ptychogonimus megastoma* (Rud.). Osservazioni sulla morfologia e fisiologia delle forme larvali e considerazioni filogenetiche. *Rivista di Parassitologia*, **6**, 117–72.

PARONA, C., 1894. L'elmintologia italiana da suoi primi tempi all'anno 1890. Storia, sistematica, corologia e bibliografia. *Atti della R. Università di Genova*, **13**, 1–733.

PARONA, C., 1912. *L'elmintologia italiana da'suoi primi tempi all'anno 1910. Bibliografia, sistematica, corologia, storia. Vol. 2: Sistematica, corologia, storia*, 540 pp. Novara.

PELSENEER, P., 1928. Les parasites des Mollusques et les Mollusques parasites. *Bulletin de la Société zoologique de France*, **53**, 158–89.

POIRIER, J., 1885. Contribution à l'historie des trématodes. *Archives de zoologie expérimentale et générale.* Serie 2, **3**, 465–624.

PRUDHOE, S. & BRAY, R. A., 1973. Digenetic trematodes from fishes. *B.A.N.Z. Antarctic Research Expedition Reports*, Series B, **8**, Part 10, 195–225.

REBECQ, J., 1965. Considerations sur la place des trematodes dans le zooplancton marin. *Annales de la Faculté des sciences de Marseille*, **38**, 61–84.

REIMER, L. W., 1974. The position of cephalopods in life cycles of helminths of marine fishes. In: *Proceedings of third international congress of parasitology*, **3**, 1727–8. Vienna: Facta Publication. [Abstract]

REIMER, L. W., GERGER, C., HENER, B., LAINKA, H., ROSENTHAL, I. & SCHARNWEBER, I., 1971. [On the distribution of larval helminths in planktonic animals of the North Sea.] *Parazitologiya (Leningrad)*, **5**, 542–50. [In Russian]

SHORT, R. B. & POWELL, E. C., 1968. Mature digenetic trematodes from New Zealand octopuses. *Journal of Parasitology*, **54**, 757–60.

STAFFORD, J., 1907. Preliminary report on the trematodes of Canadian marine fishes. *Further Contributions to Canadian Biology, 1902–1905*, 91–4.

STUNKARD, H. W., 1961. *Cercaria dipterocerca* Miller and Northup, 1926 and *Stephanostomum dentatum* (Linton, 1900) Manter, 1931. *Biological Bulletin. Marine Biological Laboratory, Woods Hole, Mass.*, **120**, 221–37.

USPENSKAJA, A. V., 1963. [Parasitic fauna of benthic crustaceans from the Barents Sea.] *Akademii Nauk SSSR (Moscow, Leningrad)*, 128 pp. [In Russian]

VAULLEGEARD, A., 1896. Notices helminthologiques. *Bulletin de la Société linnéenne de Normondie*, Serie 4, **10**, 50–60.

WAGENER, C. R., 1860. Über *Distoma appendiculatum*, *Archiv für Naturgeschichte*, **26**, 165–94.

WIRZ, K., 1958. Céphalopodes. *Faune marine des Pyrénées-orientales*, **1**, 1–59.

YAMAGUTI, S., 1942. Studies on the helminth fauna of Japan. Part 38. Larval trematodes of fishes. *Japanese Journal of Medical Sciences*, **6**, 131–60.

YAMAGUTI, S., 1970. *Digenetic trematodes of Hawaiian fishes.* 436 pp. Tokyo: Keigaku Publishing Co.

YAMAGUTI, S., 1971. *Synopsis of digenetic trematodes of vertebrates.* 1800 pp. Tokyo: Keigaku Publishing Co.

ZAIKA, V. E. & KOLESNIKOV, A. N., 1967. [On mass infection of *Sagitta elegans arctica* Aurivillus by sexually mature trematodes.] *Zoologicheskii zhurnal*, **46**, 1121–4. [In Russian]